

A Revision of the Foraminiferal Family Heterohelicidae

By Eugenia Montanaro Gallitelli¹

Introduction

THE FAMILY HETEROHELICIDAE, as established by Cushman (1927a), is accepted at present by only a few authors (Colom, 1946, Le Calvez, 1953), and they agree to accept it only provisionally. Cushman included in the family an homogeneous group of genera related to the type genus, *Heterohelix*, but he also placed in it a number of forms which actually should have been placed among the "incertae sedis" because of transitional or poorly known morphological or anatomical characters.

Emendations of this family of considerable interest have been proposed in revisions of the systematics of Foraminifera by Galloway (1933), and chiefly by Glaessner (1936, 1937, 1945), followed without fundamental change by Sigal (1952) and Pokorný (1954). But many conclusions are still unsatisfactory.

The analytical research of Loeblich (1951) on the coiling in some Heterohelicidae, and by Hofker (1951a) concerning the toothplate in *Bolivinita* and *Bolivinoidea*, must be mentioned as indicative that this confusion is partially due to an absence of knowledge of morphological and structural characters of many genera of fundamental significance in the systematics of this family. A careful restudy of all the type species is required before a new systematical arrangement can be proposed.

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Illustrations are camera-lucida drawings made by Mr. Lawrence B. Isham and Mrs. Patricia Isham, scientific illustrators, U. S. National Museum.

Material Examined

The recent visit of the writer to Washington made possible a reexamination of all the types of the Heterohelicidae Cushman, then deposited in the U. S. National Museum; almost all the type species of the various genera are there represented. Of the type species 11 are represented by holotypes, 7 by paratypes or topotypes and 5 by hypotypes. Other congeneric species more or less related to these type species have also been restudied when necessary.

The type species of *Heterohelix* Ehrenberg (*H. americana* (Ehrenberg)) and of *Plectofrondicularia* Liebus (*P. concava* Liebus) are not available; consequently, some well known related species were examined (*Heterohelix nararroensis* Loeblich and *Plectofrondicularia garzaensis* Cushman).

Three genera (*Bolivinoopsis* Yakovlev, *Nodomorphina* Cushman, and *Nodogenerina* Cushman) are represented in the Museum only by doubtfully congeneric species; of these *Bolivinoopsis* is considered an arenaceous form by Pokorný and Sigal: thus these genera have not been taken into consideration here.

The following genera have been invalidated in the present research: *Guembelina* Egger (= *Heterohelix* Ehrenberg), *Rectoguembelina* Cushman (= *Tubitextularia* Sulc), *Ventilabrella* Cushman (= *Planoglobulina* Cushman), *Bronnimannella* Montanaro Gallitelli (= *Pseudotextularia* Rzehak).

Three related and more recently described genera, which were not included in the Heterohelicidae by Cushman, are added for discussion: *Tosaia* Takayanagi, *Tappanina* Montanaro Gallitelli, and *Trachelinella* Montanaro Gallitelli.

The genus *Pseudotextularia* Rzehak is emended and a new genus, *Racemiguembelina* is proposed.

Method of Study

The examinations were made by use of the highest magnification (× 216) available for the stereobinocular. The previous use solely of low magnifications explains many of the misinterpretations in these extremely small Foraminifera.

When the arrangement of the early chambers was not otherwise clear, specimens were immersed in anise oil, a method found to be very successful in emphasizing

¹ University of Modena, Italy.

the inner structures, although any trace of external feature then becomes temporarily concealed. It is therefore difficult to make a comparative examination between external sculpture and internal arrangement of the chambers by this method.

In studying the internal structures (inner characters of the wall, columellar process, toothplate, cribrate or radiate feature of the aperture) the best results were obtained by dissection by use of dilute hydrochloric acid mixed with a small quantity of gum tragacanth glue (a method used and described by Troelsen). This method avoids a dangerous extension of the dissolution of the test as may happen when diluted acid is used alone on very tiny tests. Some of the specimens here illustrated represent dissections obtained by this method, which in many cases can be substituted advantageously for the use of thin sections, and this has made possible many corrections to previous structural interpretations.

Statistical method was only occasionally applied, for it is hardly applicable in many cases, due to the small size of the specimens and the lack of measurable elements. It was used in the investigation of the genus *Guembelina*, in order to establish the percentage of coiled specimens in the different species and so to evaluate the validity of that genus in comparison with *Heterohelix*. For this purpose, more than 3,000 specimens were statistically examined.

Systematic Relationships

With regard to previous interpretations of the relationships in the Heterohelcidae, Cushman (1927a, p. 59) described the family Heterohelcidae as follows: "Test in the more primitive forms planospiral in the young, later becoming biserial, in the more specialized genera the spiral stage and even the biserial stage may be wanting and the relationships shown by other characters; wall calcareous, perforate, ornamentation in higher genera bilaterally symmetrical; aperture when simple, usually large for the size of the test, without teeth, in some forms with apertural neck and phialine lip." With a range of variability as great as thus stated, almost every perforate foraminifer could be included. In contrast with this too wide allowance of systematic variability for the family, very subtle generic distinctions were accepted between very closely related forms, such as *Heterohelix* and *Guembelina*, which were placed by Cushman in two different subfamilies because of a distinct early coil in the first and less frequent early coiling in the latter.

Galloway (1933, p. 342) notes with some humor that "It would be suggested to consider the whole group as one without subfamilies, or to make nearly as many subfamilies as there are genera, depending upon the caprices of the systematist." But some of these genera are quite unrelated. The positions of *Pseudovigierina* and *Siphogenerinoides* were corrected by Galloway, but no substantial changes to the general arrangement of the family were suggested.

Glaessner (1936, p. 126) divided the Heterohelcidae, *sensu stricto*, into two subfamilies: the Heterohelicinae, containing *Heterohelix* and *Spiroplectoides*, and the Gumbelininae, including *Gumbelina*, *Gumbelitra*, *Tubitextularia*, and *Pseudotextularia*.

Later, Glaessner (1945, p. 86) observed: "A few families such as the Heterohelcidae and Cassidulinidae are artificial as they include genera whose structural and genetic affinities lie elsewhere." He separated some of the Heterohelcidae of Cushman into two different superfamilies: Rotaliidea (in which he placed the Gumbelinidae near the Globigerinidae and Hantkeninidae) and Buliminidae, family Buliminidae (in which he placed the subfamilies Bolivinae, Plectofrondiculariinae and Uvigerininae). In this publication he used the family name Gumbelinidae, in place of Heterohelcidae. Glaessner's subdivision was the greatest advance to date in the systematics of the so-called Heterohelcidae, for unrelated forms were here definitely separated from the globular-chambered forms related to *Heterohelix*.

Sigal (1952) and Pokorný (1954) followed Glaessner's classification in general, both these authors place the family Gumbelinidae (with *Guembelina*) in the superfamily Rotaliidea, and place the family Heterohelcidae (with *Heterohelix*) in the superfamily Buliminidae. They continued to interpret *Bolivinita*, *Bolivinitella*, and *Bolivinella* as an homogeneous group within the Heterohelcidae.

The recent tentative classification of a group of Heterohelcidae from the Upper Cretaceous of the Pyrenees, made by Kikofne (1948), is based upon such erroneous interpretations as the biseriality of *Guembelina*. Moreover, Kikofne considered only six genera, leaving undiscussed the trio *Bolivinita*, *Bolivinoidea*, and *Bolivinella*, and he failed to discuss their most important characters.

No systematic rearrangement is possible without a previous revision of the genera on the basis of their type species. In this connection some recent contributions must be mentioned. Loeblich (1951) emphasized and illustrated the presence of coiling in "*Gumbelina*," and "*Ventilabrella*," and noted the biserial, rather than triserial, initial stage in *Eowigierina*. Hofker (1951b) examined the structure of *Bolivinoidea* and the "toothplate" in *Bolivinita*, discussing new morphologic elements. Stone (1946) described the inner structure of *Siphogenerinoides* in comparison with *Siphogenerina*.

These few analytical contributions clearly demonstrate the exactness of the statement by Loeblich (1951, p. 106) that "few families among the Foraminifera contain genera as poorly known as are several genera belonging to the family Heterohelcidae."

Basis of Present Revision

The following variable elements have been considered in this study: (1) Coiling in the early stage; (2) shape of the test and arrangement of chambers in neanic and adult stage (acceleration, etc.); (3) position and shape

of the aperture; (4) presence, development and shape of the "toothplate" or columellar process.

Coiling in the early stage is present more or less frequently in: *Heterohelix americana* (fide Ehrenberg), *H. navarroensis*, *Guembelina globulosa*, *G. globocarinata*, *G. planata*, *G. striata*, *G. glabrans*, and *G. pseudotessera* (= *G. pulchra* Brotzen). Both *Heterohelix navarroensis* and *Guembelina* spp. also have a variable percentage of specimens with the early stage uncoiled. Considering that no other differences previously separated *Guembelina* from *Heterohelix* (Galloway (1933, p. 343) states that "*Guembelina* differs from *Heterohelix* only in the absence of the spiral, early stage"), there is no further reason to uphold their generic separation: consequently *Guembelina* Egger is here considered a junior synonym of *Heterohelix* Ehrenberg.

An occasional or constantly coiled early stage in *Tubitextularia*, *Pseudotextularia*, *Gublerina*, *Pseudoguembelina*, *Planoglobulina*, and the new genus *Racemiguembelina* is here demonstrated. This character is documented for each genus in the illustrations.

Loeblich (1951) demonstrated that *Eouwigerina* has no coiling in the early stage. This observation is confirmed by the present investigation and in addition three other genera, described previously as "coiled," are demonstrated to be constantly and clearly biserial: *Bolivinitella* (according to Cushman (1929, p. 28) "in the microspheric form the young [is] apparently planispiral"), *Bolivinoidea* and *Plectofrondicularia*. Among the "Heterohelicidae," therefore, coiling is present only in the genera related also by other characters to the genus *Heterohelix*.

The exact position and shape of the aperture is here described for each genus. This important character has been neglected or erroneously described in some genera; in others neither the description nor the figures give any indication as to the apertural characters. The present investigation, involving some thousands of specimens demonstrates that (1) the genera closely related to *Heterohelix* have a simple basal arched aperture as previously described; of this group, only the accelerated genus *Tubitextularia*, with an adult uniserial stage, has an obviously terminal aperture and this is always simple, without a lip; (2) a basal aperture with lip is present in *Bolivinoidea*, *Bolivinita* (the drawings by Hofker are discussed in the systematic description), and *Tappanina*; (3) a simple, open terminal aperture is present in the genera *Zeauwigerina* and *Trachelinella*; (4) a terminal aperture, reduced to an elliptical opening by internal tubercles or costae, is observed in *Bolivinitella* and *Plectofrondicularia*; and (5) a radiate cribrate aperture is observed in *Amphimorphina* and a typically cribrate aperture seems to be occasionally present in *Bolivinitella*.

No internal columellar processes (the "toothplate" of Hofker) were mentioned by Cushman (1927a, p. 64) for this family but Hofker (1951b) recently described the "toothplate" in *Bolivinita* and, less carefully, in *Bolivinoidea*. Stone (1946) illustrated the same character for *Siphogenerinoides*. In the present investigation

an internal process is also demonstrated for *Eouwigerina* and *Pseudouwigerina*. *Bolivinoidea* has no "plate" but a continuous tube arising from the first chamber. *Bolivinita* has a "plate" (spout) which is extremely variable in shape, size, concavity, position in the apertural cavity, and development in the final "spatula." In *Siphogenerinoides* the internal "tube" is actually a spoutlike discontinuous interapertural process, whose single divisions alternate in opposite tangential positions to the aperture, with the concavity always turned towards the wall. This character gives a peculiar appearance to the apertural outline, which was misinterpreted by Stone. *Eouwigerina* has a very thin columellar process, apparently tubular and continuous, beginning with the youngest stage. *Pseudouwigerina* has a discontinuous spoutlike process, which is very clear in the final chamber. Such a great variability of this inner skeleton seems to require further study in order to establish its value in the systematics of Foraminifera.

The internal characters of the wall in the genus *Bolivinoidea* were investigated by Hofker (1952), and some corrections of his observations concerning the morphology and structure of the septa are given here. In addition, it is noted here that the internal surface of the wall is irregularly tuberculate, a most distinctive peculiarity of this genus, which is thus considered entirely valid, and not synonymous with *Bolivina* as affirmed by Hofker (1951b), Glaessner (1945), Sigal (1952), and others.

Morphological Types Recognized

The present revision does not presume to give a satisfactory reclassification of all the 23 genera included by Cushman (1948) in the family Heterohelicidae. A complete revision of all the type species and of a large number of specimens is necessary; the same has to be done for the related families and superfamilies of Foraminifera and the results compared. Moreover we do not know at present which character or characters in the Foraminifera have an actual genetic value, and in this respect the research of Arnold, Grell, and others on living Foraminifera is welcome.

It is possible here only to give an emendation of the family Heterohelicidae, and a short systematic discussion of the other genera formerly included in that family, with some new information as to their structural details.

Many specimens, in addition to those here illustrated, were partially acid-treated in order to show series of transitional forms and structural details. It was impossible to illustrate all these, hence references to these additional slides in the collections of the U. S. National Museum, are given in the systematic descriptions.

The terminal aperture is found in this family, as here restricted, only as an expression of an accelerated development from a typical "guembelinoïd" genus, as in *Tubitextularia* Sulc (= *Rectoguembelina* Cushman) where the first heterohelicoïd stage is clearly visible. Five different morphological types are distinguishable:

- (1) triserial (subfamily Guembeltriinae)
 (a) constantly triserial *Guembeltria*
 (b) with proliferation *Guembeltriella*
- (2) biserial or planispiral (subfamily Heterohelicidae)
 (a) with average proportion of thickness to breadth 1:2
Heterohelix
Pseudoquembelina
Tubitzularia
- (b) proliferation in the adult stage, average proportion of thickness to breadth=1:1 *Racemiguembelina*
- (c) frequently planispiral in early stage then proliferated, average proportion of thickness to breadth 1:4 to 1:7
Gublerina
Planoglobulina
- (d) planispiral and biserial, average proportion of thickness to breadth 1.5:1 to 4:1
Pseudotetzularia

Bolivinitella, *Plectofrondicularia*, and *Amphimorphina* have in common an early biserial stage (continued to the mature stage in *Bolivinitella*), absence of a columellar process, aperture reduced by tuberculations or even subcribrate.

The subfamily Plectofrondiculariinae Cushman can be maintained, but it has no relationship to the Heterohelicidae as presently emended. We do not know how closely the apertural character is concerned with conditions of life, but the shape of the test, the biserial early arrangement of the generally flat chambers, the peculiar reduction of the lumen in the aperture, and the lack of a columellar process have led us to here consider the former subfamily Plectofrondiculariinae as a distinct family, the Plectofrondiculariidae.

Bolivinita Cushman, *Bolivinitoides* Cushman, and *Tappanina* Montanaro Gallitelli are interrelated by having the test biserial, costate or carinate; chambers not globular; aperture basal, central, narrow. Columellar processes are sinuous and discontinuous. *Bolivinitella* Marie is only an example of convergence with *Bolivinita*, and must be separated from this quite

different group, as is discussed more fully below. These three genera belong to the subfamily Bolivinitinae.

The subfamily Eouvigerininae (type genus *Eouvigerina* Cushman) is placed within the family Buliminidae after the subfamily Bolivinitinae. The original description of *Eouvigerina* is also emended, with description of an internal columellar process.

Siphogenerinoides Cushman is initially biserial, not triserial as formerly described, and must be placed only provisionally near the Eouvigerininae until more information is available as to the genetic value and the ratio of variability of the columellar process. Also, its placement in the family Plectofrondiculariidae seems at present at least premature because of the substantially different structure of the columellar process. The name *Siphogenerinoides* is not exact from the point of view of the character it recalls, as the columellar process is not a siphon but a large discontinuous spout.

Zeuuvigerina Finlay, *Trachelinella* Montanaro Gallitelli, and *Bolivinitella* Marie are biserial, with apertural neck, without columellar process, and are still *incertae sedis*, perhaps near the Bolivinitinae, from which they are distinguished by the terminal aperture and neck.

Of the Tertiary *Tosaia* Takayanagi only three paratypes were examined. It is possible that there is a trochoid initial stage, but this requires further investigations. All the specimens seen have a quite buliminoid aperture. There is no relationship to *Guembeltria* or other true Heterohelicidae; on the other hand a relationship with the Buliminidae seems quite probable.

Pseudouvigerina Cushman must be placed unquestionably in the Uvigerininae, as was done by Glaessner (1945). It has a triserial test, terminal aperture with neck and lip, columellar process, and longitudinal ornamentation. The genus is closely related to *Angulogerina*.

Systematic Descriptions

Family Heterohelicidae Cushman, 1927, emended

Test calcareous, perforate; chambers inflated, spherical, globular or reniform; early stage either planispiral, biserial, or triserial, not trochoid; serial reductions or proliferations are occasionally present; aperture relatively large, simple and basal in biserial or triserial forms, terminal only in accelerated uniserial forms. Columellar processes absent.

Subfamily Guembeltriinae Montanaro Gallitelli, new subfamily

Test triserial; chambers globular; aperture basal, arched, simple.

Genus *Guembeltria* Cushman, 1933

PLATE 31, FIGURES 1, 2

Guembeltria CUSHMAN, CONTR. CUSHMAN LAB. FORAM. RES., VOL. 9, P. 37, 1933.

TYPE SPECIES: *Guembeltria cretacea* Cushman, 1933,

Upper Cretaceous Navarro (Maestrichtian), from pit of Seguin Brick and Tile Company, 0.8 mile south of McQueeney Station, Guadalupe County, Texas.

DIAGNOSIS: Test calcareous, triserial. Chambers generally globular, more or less regularly aligned in three series throughout development. Aperture basal, arched, simple.

DISCUSSION: An examination of all the specimens of *Guembeltria* in the U. S. National Museum shows that neither initial coil nor initial biserial stage are present. Only a single specimen is dubious, but even when immersed in anise oil it does not give the appearance of a true biserial initial stage.

On the other hand, specimens where the alignment of the three series of chambers is irregular are not rare.

Guembeltria vivans Cushman, a living form, is not a true *Guembeltria*, although triserial and with globular chambers. The aperture is extremely narrow, elongated perpendicular to the suture, and turned inwards, as in certain Buliminidae (see fig. 2). *Guembeltria*

minuta Natland, also living, is not a *Guembelitra* but because of the clearly trochoid coiling probably is a Globigerinid.

Genus *Guembeltriella* Tappan, 1940

PLATE 31, FIGURES 3, 4

Guembeltriella TAPPAN, JOURN. PALEONTOL., vol. 14, p. 115, 1940.

TYPE SPECIES: *Guembeltriella graysonensis* Tappan, 1940, Cretaceous Grayson formation (Cenomanian), from Grayson Bluff, 3½ miles northeast of Roanoke, Denton County, Texas.

ORIGINAL DIAGNOSIS: "Test free, small, triserial in the early stage, similar to *Guembelitra*, later becoming multiserial on the top; chambers globular, increasing rapidly in size; sutures distinct, depressed; wall calcareous, finely perforate; aperture at base of the final chamber."

DISCUSSION: No addition to the diagnosis given by Tappan is necessary. This genus is a further development from *Guembelitra*, becoming multiserial in the adult, a development parallel to that shown by *Planoglobulina* from the *Heterohelix* group. Consequently, the separation of this genus by Tappan has the same validity as the separation of *Planoglobulina* from *Heterohelix*. It is of some interest that Tappan also noted the presence of accessory apertures in this genus. A discussion of this general character is given in the discussion of *Pseudoguembelina* Bronnimann and Brown.

Subfamily Heterohelicinae Cushman, 1927

Genus *Heterohelix* Ehrenberg, 1841

PLATE 31, FIGURES 5-20

Heterohelix EHRENBURG, Abhandl. Akad. Wiss. Berlin, p. 429, 1841.

Guembelina EGGER, Abhandl. Akad. Wiss. Munchen, Classe II, vol. 21, p. 31, 1889.

TYPE SPECIES: *Spiroplecta americana* Ehrenberg, 1844, Cretaceous, from Missouri and Mississippi, North America (not since recognized).

DIAGNOSIS: Test calcareous, biserial or planispiral in the early stage, always biserial in the adult stage. Chambers generally inflated, globular to reniform. Wall calcareous, perforate, surface smooth or striate. Aperture basal, relatively large, with simple margin.

DISCUSSION: *Heterohelix* and *Guembelina* were considered by Cushman (1927a, p. 59) as representative of two different subfamilies of the Heterohelicidae, i. e., Heterohelicinae and Guembelininae. The distinctive character was considered to be the presence in the Heterohelicinae of a coiled early stage, "forming a considerable portion of the test." For *Guembelina*, the test was indicated as "in the early stage of the microspheric form planispiral, often skipped in the megalospheric form."

Galloway (1933, p. 343) adopted the same systematic subdivision, stating that *Guembelina* "differs from *Heterohelix* only in the absence of the spiral, early

stage." Glaessner (1945) does not cite the genus *Heterohelix*.

Sigal (1952) even placed *Heterohelix* and *Guembelina* in two different superfamilies. *Heterohelix* he placed in the superfamily Buliminidea, family Heterohelicidae, subfamily Heterohelicinae, with *Bolivinoopsis* and *Nodoplanulus*—and included in the family the two subfamilies Bolivinittinae and Plectofroncdulariinae of Cushman, emended. *Guembelina* was placed in the superfamily Rotaliidea, family Guembelinidae, between the families Globorotaliidae and Elphidiidae.

Thus, the previous separation of the two genera was based substantially on the presence of a well-developed, coiled early stage in *Heterohelix*, and rare or no coiling in *Guembelina*.

Loeblich (1951) published a discussion of the phylogenetic relationships of the Heterohelicidae of Cushman, and illustrated specimens with a coiled early stage not only in *Heterohelix*, but also in *Guembelina* (*G. globulosa* (Ehrenberg)), and *Ventilabrella* (= *Planoglobulina*) (*V. carseyi* Plummer). Concerning *G. globulosa* he noted (1951, p. 108) "an extremely tiny initial coil of about five chambers, followed by 11 to 12 biserially arranged chambers," and for *Heterohelix* (1951, p. 107) "five to six chambers of the coil," with "six to eleven biserially arranged chambers." For the present study, more than 3,000 specimens of *Heterohelix* and *Guembelina* were examined under high magnification (x 216) and, when necessary, also by immersion in anise oil. No critical examination was made of the validity of the numerous species of both *Heterohelix* and *Guembelina*, as this was aside from the main purpose of this study; therefore, in the following lists there may be some specific names which may later be proven to be synonymous. The total number of specimens examined, and the number and percentage of specimens with an initial coil are given below for the various species:

Name	Specimens	Number coiled	Percent coiled
<i>G. globulosa</i>	447	113	25.3
<i>G. globocarinata</i>	1,067	175	16.
<i>G. carinata</i>	4	2	50.
<i>G. planata</i>	5	4	80.
<i>G. striata</i>	130	5	3.8
<i>G. glabrans</i>	6	2	30.
<i>G. reussi</i>	2,000	12	0.5
<i>G. pseudotessera</i> (= <i>G. pulchra</i>)	127	5	3.9
<i>G. cubensis</i>	45		
<i>G. ultimatumida</i>	15		
<i>G. venezuelana</i>	42		
<i>G. trinitatensis</i>	1		
<i>G. wilcoxensis</i>	2		

It is necessary to remark, in considering these statistical data, that only the specimens with absolutely clear coiling are indicated in the percentage of the spiral forms. Many specimens have an asymmetrical enlargement of the test, with a slightly curved initial stage and sometimes an additional asymmetrical chamber near the proloculus. Nevertheless they were not added to the "spiraling" list. Many specimens from the early upper Cretaceous (ex. *G. moremani* Cushman) have a poorly preserved test, commonly

crystallized, so that a determination of the early stage is almost impossible. Many specimens have a very tiny coiled stage and the two or three tiny chambers below the proloculum may be partially or entirely destroyed, resulting in a falsely biserial appearance. Examples of this modification are not rare in the collection. In spite of these negative elements, and of the precautions taken in the statistical examination, the percentage of coiled specimens in more than 3000 specimens of *Guembelina* is only 8.2 percent, a value that, with further investigation, may increase but will not decrease.

Guembelina globulosa, *G. globocarinata*, and *G. planata*, are the most closely related by general shape to typical *Heterohelix*. In *G. globulosa* 25 percent of the specimens are coiled; in *G. globocarinata*, 16 percent. In many cases the well developed specimens also have well developed coiling. Nine of the 14 species of *Guembelina* examined may have a clearly coiled early stage, and although most of the paratypes of *Heterohelix navarroensis* Loeblich were found to be coiled, some uncoiled specimens also occur in this species.

In the present study only the early Cretaceous *Guembelina* have been found to be without coiling in the early stage, or show it only rarely. The name *Heterohelix* could thus possibly be restricted to only the coiled forms of the uppermost Upper Cretaceous. However, the name *Guembelina* could not be used for the uncoiled species of the Lower Cretaceous because the type species of *Guembelina* shows an early coil and is late Upper Cretaceous in age.

Morphologically, their separation is also unwarranted, because not only *Guembelina* and *Heterohelix* have an early coiled stage, as was demonstrated previously by Loeblich for *Guembelina* and *Ventilabrella* (= *Planoglobulina*), and as the present study has shown also for *Tubitextularia*, *Pseudoguembelina*, *Gublerina* and *Racemiguembelina*. Furthermore the entire group of the biserial *Heterohelicidae* (*Guembelina-Heterohelix*) are homogeneous in all other characters: the chambers tend to become globular, the surface may become striate by the alignment of the very fine spines in thin striae; there may be an initial coil of as many as 5 to 6 chambers, and there is a simple aperture.

Other differences are only minor, such as the statistically larger number of biserial chambers in *Guembelina* (in fact Loeblich cites *Heterohelix navarroensis* with 11 biserial chambers also, and the present writer observed a specimen of *G. globulosa* (Cushman Coll. 24400), with only four chambers following the coil), and the larger frequency of coiled specimens in *Heterohelix* (which has however fewer representatives in species and specimens). These differences can only justify specific separation. Consequently *Guembelina* cannot be separated from *Heterohelix* as representing a different superfamily, family, or subfamily, and is not even a distinct genus. As *Heterohelix* has priority, the name *Guembelina* must be considered a junior synonym.

Genus *Pseudotextularia* Rzehak, 1891, emended

PLATE 33, FIGURE 6

Pseudotextularia RZEHAK, Verh. Naturf. Ver. Brünn, vol. 24, p. 8, 1886 (nomen nudum); (part), Ann. Naturhist. Hofmus., Wien., vol. 6, No. 1, p. 2, 1891.

Bronnibrownia MONTANARO GALLITELLI, Mem. Accad. Sci. Lett. Arti Modena, ser. 5, vol. 13, pp. 215, 220, 222 (nomen nudum), 1955.

Bronnimannella MONTANARO GALLITELLI, Contr. Cushman Found. Foram. Res., vol. 7, p. 35, 1956. Type species: *Guembelina plummerae* Loetlerle, 1937; fixed by original designation.

TYPE SPECIES: *Cuneolina elegans* Rzehak, 1891. Fixed by subsequent monotypy, Rzehak, 1891. From the Upper Cretaceous (Alttertiär, Paläogen), glaukonitischer Tegelsand, from Bruderndorf, Niederösterreich, Germany.

DIAGNOSIS: Test calcareous, generally coiled in the early stage, later biserial, cuneiform, chambers rapidly increasing in size as added. Later chambers increase very rapidly in thickness and become comparatively strongly compressed laterally, so that the original proportion of breadth to thickness is inverted, reaching an extreme of 1 : 4. The last chamber may be deflected from the normal biserial alignment and become nearly central in position. Aperture broad, becoming almost linear in the most appressed forms. Aberrant specimens may have an additional smaller aperture at the top of the last chamber.

DISCUSSION: The generic name *Pseudotextularia* was first used by Rzehak (1886, p. 8) for a form resembling *Textularia*, but regarded as either a monstrosity or a new genus. No species were placed in the genus until 1891 (p. 4) when Rzehak described *Cuneolina elegans*, remarking that it should perhaps be placed in a distinct genus, for which he had previously proposed the name *Pseudotextularia*. *Cuneolina elegans*, as the first species placed in the genus, thus becomes the type species, as was noted by Ellis and Messina (1940), being designated by subsequent monotypy. Rzehak included in this species both biserial forms and those with chamber proliferation. He later (Rzehak, 1895, p. 217) described *Pseudotextularia varians*, but as he included his earlier *Cuneolina elegans* in its synonymy, *P. varians* is an invalid synonym. This publication gave the earliest illustrations, the figs. 1a, b being of a biserial specimen, and figs. 2, 3 showing a form with chamber proliferation at the top. This description considered the biserial form to represent a youthful stage of a species whose adult form was proliferated. Later workers considered them to represent two different species, and White (1929, p. 40) restricted *Pseudotextularia varians* to the figs. 2, 3 of Rzehak, and placed the biserial form (Rzehak's figs. 1a, b) in *Guembelina elegans* (Rzehak).

Galloway (1933, p. 348) considered *Pseudotextularia varians* to be the type by monotypy of *Pseudotextularia*, also considering Rzehak's fig. 1 to be of *Guembelina elegans*; in this he was followed by later writers (Cushman, 1948, p. 256; Pokorný, 1954, p. 245).

Glaessner (1936, p. 99) considered *varians* to be only a variety of *elegans*, and copied Rzehak's figs. 1a, b as typical *Pseudotextularia elegans*, Rzehak's fig. 2 as *P. elegans* var. *varians*, and Rzehak's fig. 3 as *P. elegans* var. *aeruvulinoides* (Egger). Glaessner included within *Pseudotextularia* Rzehak, 1891, both the forms with and without proliferation, included therein by Rzehak, and also the genera *Planoglobulina* Cushman, 1927, and *Ventilabrella* Cushman, 1928, which also show chamber proliferation. *Ventilabrella* is here considered to be a synonym of *Planoglobulina*, but the latter is regarded as distinct from both *Pseudotextularia* and the new genus here described as *Racemiguembelina*.

As mentioned above, the type species of *Pseudotextularia* is *Cuneolina elegans*, and the lectotype of the type species is Rzehak's figs. 1a, b from the description of *Pseudotextularia varians*. As mentioned above and as noted by Ellis and Messina (1940), *P. varians* is merely a junior synonym of *C. elegans*, and the proliferated form requires a new name.

Following the earlier but erroneous type designation by Galloway, Cushman, Ellis and Messina, and others, the present writer recently proposed the generic name *Bronnimannella* for the biserial species with later lateral compression, type *Guembelina plummerae* Loetterle. The designation of the type specimen of *Pseudotextularia elegans* as Rzehak's fig. 1 of the 1895 publication, makes the species *Guembelina plummerae* Loetterle a junior synonym, as it is of similar size, proportions and ornamentation. Thus, the type species of *Bronnimannella* is conspecific with the type of *Pseudotextularia*, and the generic name *Bronnimannella* becomes a junior subjective-objective (genotype species are believed to be the same) synonym.

The early stage suggests the relationship of *Pseudotextularia* to *Heterohelix*, but in the mature test a gradual but complete change occurs in the proportion of breadth to thickness, with extreme specimens having the proportion of breadth to thickness of 1:4. Possibly another species could be separated, representing the maximum lateral constriction (1:5.5), but a careful investigation of several hundred specimens of the species did not show any sharp discontinuity between the moderately and strongly compressed specimens, although the two extremes look quite different in shape. The ornamentation consists of similar axial ridges, sometimes more prominent in the young stage, and the initial coil is frequent both in the less and in the more compressed forms. Also the deflection of the final chamber to a central position is found in specimens of both extremes of the lateral compression. An example with final central chamber was illustrated recently as *Bronnimannella plummerae* (Loetterle) (by Montanaro Gallitelli, 1956) and hence is not here refigured.

The constant characters of this genus are a distinctive lateral compression of the test, of great or lesser intensity, culminating in an inversion of the usual proportion of breadth to thickness as known for the

Heterohelicidae; and a biserial arrangement of the adult chambers.

Pseudotextularia differs from *Planoglobulina* in the inversion of the proportions of lateral compression of the test, and an absence of chamber proliferation. *Racemiguembelina*, new genus, is separated from *Pseudotextularia* by the conical shape (proportion of breadth to thickness of 1:1) and the crown of chamberlets at the top of the test.

The perfect preservation and the normal increase in the young stage of all the specimens exclude the possibility of mechanical deformation of the test during fossilization.

Kikoïne (1948, pl. 1, figs. 5 and 8) figured specimens of this genus from the Upper Cretaceous of Hendaye and Gan (Southern Pyrenees). He interprets the specimen of his figure 8 as a new variety of *Guembelina striata* (Ehrenberg), *G. striata* var. *deformis* Kikoïne, and noted that this variety represents "l'aboutissement de l'évolution de *G. plummerae*," and that only the ornamentation of the variety is comparable with the species *striata*. The figures given by Kikoïne clearly show his form to be identical with *G. plummerae* (= *Pseudotextularia elegans*), and his variety invalid.

Genus *Pseudoguembelina* Bronnimann and Brown, 1953

PLATE 31, FIGURES 21-23

Pseudoguembelina BRONNIMANN and BROWN, Contr. Cushman Found. Foram. Res., vol. 4, pt. 4, p. 150, 1953.

TYPE SPECIES: *Guembelina excolata* Cushman, 1926. Upper Cretaceous Mendez shale, from Mexico.

DIAGNOSIS: Test biserial, rarely may be coiled in the early stage; chambers subglobular, becoming lobate in the mature test and compressed laterally near the aperture. Wall calcareous; surface with straight longitudinal costae. Aperture arched, sinuous, extended down into the lateral lobes of each mature chamber, and producing a sort of accessory aperture which may be covered by tiny flaps.

DISCUSSION: The presence and the frequency of accessory apertures in the different genera of the Heterohelicidae has been studied, as a basis upon which to confirm or deny the validity of the genus *Pseudoguembelina*. Accessory apertures may occasionally be present in the penultimate or last chamber of various globose species, but it is always a rare feature. Such is the case for *Guembelina striata*, where the accessory apertures are not the rule. Rare accessory apertures were also observed by Tappan in *Guembeliriella* Tappan, are not rare in *Ventilabrella*, and can also be observed in *Pseudotextularia elegans* (Rzehak). Consequently, as this character is not constant, with related peculiarities of shape and position, and as it is not accompanied by other constant morphological or structural characters, it cannot be accepted as a character of generic importance.

However, in *Pseudoguembelina costulata* (Cushman),

P. excolata (Cushman) and *P. palpebra* Bronnimann and Brown, the accessory apertures are present from the very first stages, are connected with a peculiar feature of the chambers, and, finally, have a quite different appearance from the accessory apertures we observe occasionally in other *Heterohelicidae*. A specimen of *P. costulata* was chosen to show the peculiarity of this character. The reniform chambers become constricted near the axial area, then extend laterally in two lobes, which are tubuliform when well developed, and curved to meet the lower chambers. When the lobes are small, one may observe (fig. 22) that they originate from a conspicuous extension of the aperture, with two more or less marked constrictions near the two lateral extremities of the aperture. In such a situation, the chambers lose their original globular appearance. The morphological transition from globular to reniform to lobate chambers may be observed in the populations of *Heterohelix* (*Guembelina*) *globulosa* and *H. planata*, and *H. pseudotessera* (= *H. pulchra* (Brotzen), 1936; see Montanaro Gallitelli, 1955b, p. 188). Consequently, the genus *Pseudoquembelina* Bronnimann and Brown is considered to be a valid genus, but is restricted to include only those forms with a strong modification in the shape of the terminal basal part of the chambers and of the aperture, which give rise to peculiar accessory apertures, differing in their origin from the accessory apertures occasionally found in other species and genera of the *Heterohelicidae*. For this reason, *P. striata* and *P. punctulata* are not considered to be typical *Pseudoquembelina*, but are here considered to belong to *Heterohelix*.

Bronnimann and Brown (1953, p. 153) stated that "*Textularia striata* Ehrenberg is the only species of *Pseudoquembelina* n. gen. in which coiling has been observed." The present study has shown that it occurs also in *P. excolata* (Cushman), the type species of the genus (fig. 23).

Genus *Gublerina* Kikoïne, 1948

PLATE 32, FIGURES 1-9

Gublerina KIKOÏNE, Soc. Géol. France, Bull., ser. 5, vol. 18, fasc. 1-3, p. 26, 1948.

TYPE SPECIES: *Gublerina cuvillieri* Kikoïne, 1948 (= *Ventilabrella ornatissima* Cushman and Church, 1930), Upper Cretaceous (Maestrichtian), from the region of Orthez and to the south of Gan, northern edge of the Pyrenees, France.

DIAGNOSIS: Test compressed, rapidly increasing in breadth but not flabelliform, presenting a fairly broad triangular outline. Early stage frequently coiled; in the later stage the chambers are arranged in two diverging series, commonly widely separated by a broad, nonseptate, incompletely divided or occasionally bubbled central area which only finally becomes camerata. Proliferation of chambers occurs at the top of

the test, with 4-8 final bulbous chambers. Sutures well developed, limbate, generally granulate on the surface, sometimes strongly projecting. Wall calcareous, surface opaque, rough, especially in the early stage, except for the initial coil which is generally smooth and transparent. Aperture not visible in the paratypes available.

DISCUSSION: Comparison of the holotype and paratypes of *Ventilabrella ornatissima* Cushman and Church with the topotypes of *Gublerina cuvillieri*, in the National Museum collections, showed that the specific name *cuvillieri* is also invalid as it is a synonym of *Gublerina ornatissima* (Cushman and Church). The morphologic characters of this genus brought out in this paper prove its validity, although the genus must be somewhat emended from the original description. Recognition of these characters was made possible by etching away in hydrochloric acid the external part of the wall in two specimens of *Gublerina cuvillieri* (= *G. ornatissima*).

Thus, a coiled early stage may be present (fig. 3), followed by the young biserial stage. The first two to four pairs of chambers are overlapping, then the two series of chambers become more and more divergent, leaving a broad internal communication between the chambers and the wide undivided central cavity (fig. 7). True internal chambers are not developed at first in this central area, which becomes irregularly more or less "bubbled" in appearance (fig. 4). The granulated, suturelike median costae were dissolved at the surface by hydrochloric acid in order to verify the presence of a median series of chambers, but no internal chambers were found to correspond with these superficial costae (fig. 2). Another partially dissolved specimen (fig. 1) and three complete specimens (figs. 5, 7, 3) show the sequence from a flat, depressed, and unornamented central area to a subcostate to a final bubbled one. In figure 4 granulated intermediate costae and the final polycamerate stage can be seen.

A specimen of *Ventilabrella ornatissima* Cushman and Church, similarly treated (figs. 6a, b), shows that the two series of chambers openly communicate in the central area, and that a third incomplete arched suture appears in the central area, immediately below the final proliferation.

Ventilabrella decoratissima de Klasz is a *Gublerina* with strongly developed granulated sutures, and a biserial arrangement of chambers nearly to the top of the test, which shows the usual final proliferation. Paratypes of this species from the Santonian of Eisenärzt, Bavaria (de Klasz Coll.) show the *Gublerina*-arrangement of the chambers and the surface sculpture (fig. 8).

The constant characters of *Gublerina* are, therefore, the biserial arrangement of the chambers almost to the top of the test, with the two gradually diverging series separated by an intervening noncamerate cavity; and the limbate sutures, frequently granulate on the surface,

opening internally and leaving a broad opening between the chambers and the central area. *Gublerina* thus represents one of the most distinctive genera in the family Heterohellicidae.

Variable characters are (1) the width of the central cavity, where an incomplete central chamber occasionally appears, and the broad opening from the chambers into the wide central cavity; (2) the development of the granulated ornamentation; (3) the presence, size, depression, and evidence of bubbles in the central area; and (4) the external lateral inflation of the chambers and consequently the sharpness of the transverse section. A comparison of *G. ornatissima* and *G. decoratissima* emphasizes the constant and the variable characters of this very distinctive genus.

Some other synonyms of species of *Gublerina* have been suggested by Bronnimann and Brown (1954). *Gublerina hedbergi* Bronnimann and Brown was stated to be a synonym of *G. acuta robusta* de Klasz, and *Gublerina* aff. *G. cuvillieri* Kikoine described by de Klasz (1953, p. 248, footnote 1, pl. 8, figs. 2a, b) is the same as *G. glaessneri* Bronnimann and Brown.

The investigation of the structure of the central area of the test, and the statement that central internal chambers do not occur in *Gublerina* but are so simulated by more or less irregular bubbles and external ornamentation, suggest the advisability of reexamining many of the specimens interpreted as *Gublerina* and figured with one or more completely developed central chambers. Such a character (central internal chambers), when actually occurring in flabelliform specimens, represents *Planoglobulina*, not *Gublerina*. On the other hand, specimens where the reniform chambers are arranged in two diverging series, separated by a nonseptate central area but without proliferation at the top of the test, are representatives of aberrant forms (although still of *Gublerina*) which tend toward the extreme limits of variability of the genus *Heterohelix* (*H. tessera*, *H. pulchra*, *H. lata*).

A paratype of *Gublerina hedbergi* (= *G. acuta robusta* de Klasz) examined for this study shows that following an early coiled stage there are eight chambers with a typical guembelinoid development (chambers inflated and sutures deep and narrow). The four mature chambers which follow become reniform and depressed in the central area, simulating, because of their irregularity, the presence of one or more internal chambers. Actually an observation of both sides of the test by transmitted light shows no traces of sutures in this area. The fragmentary final two chambers in this paratype show only a bicamerate end stage, not multicamerate as in *Gublerina*, even though the wide central area, typical of this genus, is present. A comparison with forms like *Heterohelix pseudotessera* (= *H. pulchra*) and *H. lata* can be made through the illustrations given here.

Thus, the genus *Gublerina* can be interpreted as very distinctive, with its morphological and genetical position between *Heterohelix* and *Planoglobulina*.

Genus *Planoglobulina* Cushman, 1927

PLATE 32, FIGURES 10-13

Planoglobulina CUSHMAN, Contr. Cushman Lab. Foram. Res., vol. 2, p. 77, 1927.

Ventilabrella CUSHMAN, Contr. Cushman Lab. Foram. Res., vol. 4, p. 2, 1928.

TYPE SPECIES: *Guembelina acervulinoides* Egger, 1900. Upper Cretaceous Senonian of Bavarian Alps. Numerous localities and horizons were listed, none designated as type. The synonymous *Ventilabrella* was also defined without citation of a type specimen, horizon, or locality in either the generic definition or the description of the type species, *V. eggeri* Cushman.

DIAGNOSIS: Test biserial in the young stage, later with a more or less abundant proliferation of globular chambers, which spread out in the plane of biseriality, giving a flabelliform shape to the test. Wall calcareous, finely perforate, and commonly striate on the surface. Aperture multiple on the final series of chambers, which may be numerous.

DISCUSSION: This genus can easily be distinguished from *Gublerina* by the absence of costate sutures and the globular and completely developed chambers in the area of proliferation.

A comparison of the figures of complete and sectioned specimens of *Gublerina* and *Planoglobulina* emphasizes these differences better than does a discussion. Specimens from the Cushman Collection (31839 and 31861) also demonstrate these elements well.

According to the present redescription and emended diagnosis of the genus *Gublerina*, *Ventilabrella decoratissima* de Klasz is a typical *Gublerina*. The figure given by de Klasz (1953) seems to represent a real *Ventilabrella* (= *Planoglobulina*). However, examination of a paratype in the de Klasz collection in the U. S. National Museum, shows somewhat different ornamentation and character of chambers, and an internal structure typical of a *Gublerina*.

A young specimen of *Planoglobulina eggeri* (Cushman) var. *glabrata* (Cushman) shows the derivation of *Planoglobulina* from a *globulosa*-like *Heterohelix*.

The generic name *Ventilabrella* has commonly been used for this group of species, but is a synonym of *Planoglobulina*. Both genera were described by Cushman, who stated that *Planoglobulina* arose from a *Pseudotextularia* stage and *Ventilabrella* from a *Guembelina* stage. *Planoglobulina* was defined in 1927, and the type designated as *Guembelina acervulinoides* Egger. Cushman (1927b) stated that it had a planospiral early stage, followed by a biserial stage and finally a proliferation of chambers in a single plane. The following year Cushman (1928) defined *Ventilabrella*, citing as type the new species *V. eggeri*, and stating that it developed from a biserial stage, with later proliferation of chambers in a single plane. In his description of the type species he also stated that the microspheric form probably also was planispiral in the early stage.

Within the description of *Ventilabrella eggeri*, Cushman (1928) also discussed *Planoglobulina* and selected Egger's figure 20 as the type of the species *P. acervulinoides* Egger. This specimen shows well developed proliferation following a biserial early stage. The figure is not sufficiently clear to note the presence or absence of an early coil. Although he selected a type for Egger's species, Cushman apparently neglected to do so for *V. eggeri*, for no holotype or paratype specimens of *V. eggeri* occur in the Cushman collection or U. S. National Museum collections, and no type specimen is listed in the text in this or later papers of Cushman. Furthermore, no type horizon or locality were cited for *V. eggeri*, although Cushman stated (1928, p. 3) that "species of *Ventilabrella* occur often in great numbers in certain horizons of the Taylor marl of Texas."

In 1946, Cushman did illustrate specimens of *V. eggeri*, from the Taylor, but also placed in the synonymy of *V. eggeri*, *Planoglobulina acervulinoides* Egger (part), and included Egger's figure 20! He thus placed the specimen he himself had selected as type for Egger's species in his later species, so that the type species of *Ventilabrella* (*V. eggeri*) is a junior synonym of the type species of *Planoglobulina* (*P. acervulinoides*), the two genera thus being identical.

Galloway (1933) placed *Ventilabrella* in the synonymy of *Planoglobulina*, but was not followed in this by most other workers, who recognized both genera. Species referred to the two generic names are identical in development, with a biserial stage, or more rarely coiled to biserial, followed by chamber proliferation in a single plane, resulting in a flabelliform test.

As *Planoglobulina* has priority, and the type species are synonymous, the name *Ventilabrella* must be suppressed as a junior subjective-objective (genotype species are believed to be the same) synonym.

Genus *Racemiguembelina* Montanaro Gallitelli, new genus

PLATE 32, FIGURES 14, 15

Pseudotextularia RZEHAK (part), Ann. Naturhist. Hofmus. Wien, vol. 6, No. 1, p. 2, 1891.

TYPE SPECIES: *Gümbelina fruticosa* Egger, 1900, Upper Cretaceous (Senonian) of Bavarian Alps, Germany.

DIAGNOSIS: Test calcareous, conical in shape; rarely planispiral in the early stage, later biserial, increasing regularly and equally in thickness and breadth, finally proliferated with a varying number of additional globular chambers, the last of which form a crown at the top of the test and are provided with a series of arcuate, basal apertures. No spiral arrangement of the adult chambers is evident. Ornamentation consists of longitudinally developed costae.

DISCUSSION: This genus includes species that develop a final chamber proliferation, giving rise to a conical

test, such as have been placed in the genus *Pseudotextularia* Rzehak by various authors. As the emendation of the genus *Pseudotextularia*, earlier in the present paper, on the basis of its type species, *P. elegans* (Rzehak), restricts that genus to species which are biserial in the adult, with a lateral compression of the test in its later stages, the forms with chamber proliferation require a new generic assignment, and the present genus is proposed to fill that necessity.

As noted above, in the discussion of *Pseudotextularia*, specimens of this type were originally included with specimens of a biserial genus in Rzehak's description (1891, p. 2) of *Cuneolina elegans*, and later both forms were figured by Rzehak (1895) as *Pseudotextularia varians*.

Because Rzehak (1895) included in his synonymy of *Pseudotextularia varians*, the prior name *Cuneolina elegans*, he obviously considered them identical, hence the specific name *variens* must be suppressed as a junior synonym of *elegans*, as was later noted by Ellis and Messina (1940). It cannot be later resurrected for part of the group included therein by Rzehak. The biserial specimen of Rzehak (1895, pl. 7, fig. 1) was referred to the restricted *Cuneolina elegans* (= *Pseudotextularia*) by White (1929, p. 40), and is thus the lectotype of that species.

Cushman (1938, p. 22) considered *Gümbelina fruticosa* Egger (misspelled as *fruticosa*) to be identical with *Pseudotextularia varians*. Thus the first valid name available for the proliferated form of Rzehak (commonly but erroneously referred to previously as *Pseudotextularia varians*), is *fruticosa*, and the correct name thus becomes *Racemiguembelina fruticosa* (Egger).

The enlargement of the test in *Racemiguembelina* produces a form which is circular or subcircular in transverse section. This circular section, together with the high degree of chamber proliferation in the mature stage, are characters, peculiar to this genus, which justify its separation from those forms with a completely biserial chamber arrangement and lateral compression.

If we do not consider as generic distinctions both these peculiarities—the conical enlargement and the final proliferation of the chambers, and accept within its range of variability the forms without proliferation and also those more or less compressed or extended, the majority of the globular-chambered Heterohellicidae could be placed within a single genus. As there is no biological proof to confirm or deny the "natural" value of these characters in extinct forms, we must accept the morphological features of the test as a basis for a usable taxonomy, and the compressed biserial forms are here considered to belong to the genus *Pseudotextularia*, emended, whereas those with chamber proliferation belong to the present genus *Racemiguembelina*.

Although many authors cite a spiral arrangement of the chambers in this proliferated genus, none is visible either in their published figures nor in the types examined, hence this is discounted.

The generic name comes from *racemus*, Latin, bunch or cluster of grapes + *Guembelina*, genus of Foraminifera; gender, feminine. The name refers to the later chamber proliferation as in a bunch of grapes, following an early development like *Guembelina* (= *Heterohelix*).

Genus *Tubitextularia* Sulc, 1929

PLATE 33, FIGURES 1-5

Tubitextularia SULC, Vestnik Stát. Geol. Českosl. Rep., vol. 5^o p. 148, 1929.

Rectoguembelina CUSHMAN, Contr. Cushman Lab. Foram. Res., vol. 8, p. 6, 1932.

TYPE SPECIES: *Pseudotextularia bohémica* Sulc, 1929, Upper Cretaceous Senonian, of Vinice, Czechoslovakia.

DIAGNOSIS: Test with initial stage coiled or more commonly biserial, consisting of two to eight chambers followed by an uniserial stage of two to five chambers. Chambers inflated. Wall calcareous, perforate, smooth. Aperture simple, terminal.

DISCUSSION: The genus *Rectoguembelina* Cushman has identical characters and is a synonym of *Tubitextularia* as was correctly stated by Glaessner (1936, p. 108). The only differing character cited by Cushman is the presence of a neck in *Rectoguembelina*. However, even the figure given by Cushman (after Sulc) shows the last chamber in *Tubitextularia*, as in *Rectoguembelina*, becoming elongate and rather constricted in a sort of large neck, which is broken. Consequently only a specific separation can be admitted. This genus can be considered as an example of genetic reduction in the number of chambers, which has a parallel in other families. The modification of the apertural position from basal to terminal is an obvious consequence of the change in chamber arrangement. Other than position, the character of the aperture is identical to that of other Heterohelicidae, i. e., simple, without lip, tooth, or internal laminae. That it is clearly derived from a heterohelicoid form is shown by the occasional remnant of the primitive basal aperture at the end of the young biserial stage.

In addition to the type species, only *Tubitextularia cretacea* (Cushman) and *T. texana* (Cushman) definitely belong to this genus, as shown by the clearly heterohelicoid young stage. A much accelerated specimen identified by Cushman as *T. texana*, has only a coiled first stage followed, without a biserial stage, by a uniserial stage of four chambers. Another specimen has only three initial chambers which are doubtfully biserial with an oblique axis before the uniserial stage. In this latter example, the heterohelicoid stage has practically disappeared but there are all gradations from the genus *Heterohelix* (*H. globulosa*) to *Tubitextularia*, which can thus be interpreted as an aberrant development of *Heterohelix*, but not as a stratigraphical evolution from it.

Family Plectofrondiculariidae Cushman, 1927

Subfamily Plectofrondiculariinae Cushman, 1927

Genus *Bolivinella* Cushman, 1927

PLATE 33, FIGURES 12-13

Bolivinella CUSHMAN, Contr. Cushman Lab. Foram. Res., vol. 2, p. 79, 1927.

TYPE SPECIES: *Textularia agglutinans* d'Orbigny var. *folium* Parker and Jones, 1865, from Recent shore sand, near Melbourne, Australia.

DIAGNOSIS: Test biserial, compressed, flabelliform. Proloculum spherical in megalospheric specimens, elongate or ovoidal, provided with one or two spines. No coiling present. Chambers depressed, slightly overlapping, narrow and much elongate laterally, generally sigmoid. Sutures well developed, limbate, more or less projecting. Wall calcareous, perforate. There is no simple basal aperture, but a series of tiny openings at the base of the final chamber, surrounded by numerous papillae commonly aligned in series radiating from the apertural area.

DISCUSSION: The genus is placed by Galloway and Cushman near *Bolivinella*, in the Bolivinittinae. Sigal maintains its placement in the Heterohelicidae (superfamily Buliminidea). Pokorný puts *Bolivinella* in the same superfamily, but in the subfamily Plectofrondiculariinae.

Galloway (1933, p. 350) referred to the early stage as "in the microspheric forms doubtfully planispiral" and Cushman (1927b, p. 79) described the aperture as "transverse to the compression of the test, with numerous papillae at the base of the opening".

Sigal (1952, p. 224) considers *Bolivinella* closely related to *Bolivinella* and *Bolivinella*, as all the three genera "sautent le stade planispirale." The present research, made at high magnification on several hundred specimens and sections now gives a more complete documentation of the morphological characters. As stated by Sigal, a coiled initial stage is definitely excluded, as none was shown in the specimens examined. The proloculum is spherical, ovoidal, or reniform; provided with one or two spines, and partially broken spines give the appearance of the "rectangular" proloculum described by Cushman. Partial dissolution by hydrochloric acid shows the two symmetrical chambers following the proloculum.

New information is available concerning the aperture. The original figures of the type species show a generalized simple aperture, as Cushman (1927b, p. 79) described vaguely. The diagnosis of the numerous species of Cushman give no description or figure of the aperture. The aperture consists of a row of small openings at the central part of the base of the final chamber. Investigation of the apertural area has been

made either at a magnification of $\times 216$ with the stereobinoocular microscope or with transmitted light. Acid treatment has also been used to make the apertural area visible and free of ornamentation. The aperture consists of 2 to 4 minute openings aligned at the base of the final chamber and the adjoining upper surface is covered by numerous papillae or minute spines aligned in radiating rows. These rows continue over the entire apertural face, the ridges running between the pores at the base of the face and touching the opposite chamber surface. An open elongate aperture, as described by Cushman and figured by Parker and Jones, is visible only when the specimen has been damaged, and is not present in any stage of the development of the test, as proved by dissection of specimens. The tiny apertural openings are visible only at high magnification, but this apertural character and the radiating papillae are both present in different species, demonstrating that they do not represent an abnormality. The amount of ornamentation and the number and size of the pores are variable characters.

Concerning the ornamentation, Cushman considers the lateral spines to be frequent, those of the proloculum rare. However, the spines of the proloculum represent the rule, and the lateral spines, sometimes modified into alar expansions, represent a specific character, and may be absent altogether. As is understandable, no toothplate is present in this genus.

The completely different apertural character as here described proves that no relationship exists between *Bolivinitella* and the groups of *Bolivinita* and *Bolivinitella*.

Genus *Plectofrondicularia* Liebus, 1903

PLATE 33, FIGURES 10, 11

Plectofrondicularia LIEBUS, Jahrb. Geol. Reichs., vol. 52, p. 76, 1903.

TYPE SPECIES: *Plectofrondicularia concava* Liebus, 1903, Tertiary (upper glass sand) Promberger Schichten?, from Probe 69, southeast of Heimberg bei Meisbach, Oberbayern, Germany.

DIAGNOSIS: Test elongate or frondicularian, biserial in the early stage, later uniserial, much compressed; sutures limbate. Wall calcareous, smooth or longitudinally costate; aperture terminal with an elliptical margin, internally depressed and radially dentate: the teeth are frequently anastomosed at the interior of the aperture, which becomes reduced to one or more small, irregularly distributed, elliptical openings.

DISCUSSION: No specimens of the type species were available in the U. S. National Museum and the figures given by Liebus show an incomplete specimen with an early biserial stage. Nevertheless, Cushman describes a planispiral early stage for the genus. An examination of all specimens of other species of *Plectofrondicularia* in the National Museum showed none with an early coiled stage. In the elongate forms the biserial stage has a *Bolivina*-like arrangement; in the more enlarged species (*P. garzaensis* Cushman and Siegfus) the first two or three chambers embrace the proloculum. This arrange-

ment, which must not be confused with a planispiral development, is here illustrated. The third chamber is then placed above the first two chambers, and is followed by the symmetrical uniserial development of the mature stage.

The aperture was previously described only as terminal, elliptical. The elliptical lip is easily visible and may be rather well developed. The aperture is concave; the lip is internally thickened, with a variable number of radiating teeth which reach the center of the aperture and may become anastomosed there, so that the aperture is reduced to one or more small openings. No internal tube or toothplate are present. This apertural character is identical in different species (*P. floridana*, *P. californica* and *P. garzaensis*), so that it may be considered a constant character of generic significance.

The character of the aperture and the first stage of the test both show a relationship to the completely biserial *Bolivinitella*, and demonstrate that there is no relationship between these genera and the *Heterohelicidae*, s. s.

Glaessner (1945) placed *Plectofrondicularia* in his superfamily Buliminidea, family Buliminidae, subfamily Plectofrondiculariinae, and in this was followed by Pokorný (1954). Sigal (1952) considered this genus to belong to the Heterohelicidae, with *Bolivinitella*. The subfamily is here elevated to family status.

Genus *Amphimorphina* Neugeboren, 1850

PLATE 33, FIGURES 7-9

Amphimorphina NEUGEBOREN, Verh. Mitth. Siebenbürgischer Ver. Naturw., vol. 1, p. 125, 1850.

Nodomorphina CUSHMAN, Contr. Cushman Lab. Foram. Res., vol. 2, p. 80, 1927.

TYPE SPECIES: *Amphimorphina hauerina* Neugeboren, 1850, Miocene, from Lapugy, Hungary.

DIAGNOSIS: Test elongate, more or less compressed in the early stage, which is uniserial in the megaspheric form and clearly biserial in the microspheric form, including the six to ten early chambers. Chambers frondicularian in the young stage, then may be inflated; sutures limbate and centrally crossed by a rather large lumen. Ornamentation longitudinal, with more or less lamellate costae, situated near the margins of the test. Aperture in the early stages consists of grooves radiating from the center, and in the later stages consists of 3 to 6 pores separated by the converging ribs, which meet terminally.

DISCUSSION: The biseriality of the early stage of the type species of *Amphimorphina* was not noted by Neugeboren, although Cushman (1927, p. 63) stated that the microspheric form "may show traces of the biserial stage."

There is nevertheless a clearly biserial early stage, as shown in the figures. One specimen was observed which has a single asymmetrical chamber following the proloculum, that could be interpreted as a subcoiled stage, but in reality it is only an abnormal accelerated increase giving rise immediately to a third

completely developed chamber which occupies the full breadth of the test. Megalospheric specimens are also figured for the same species.

Neither Neugeboren nor Cushman figured complete specimens. The aperture in the early stages consists of radiating grooves from the mid-point of the apertural region. The ribs between these grooves converge in later growth, meeting centrally and leaving open 3 to 6 pores between the strong radial costae, forming a cribrate aperture. A similar aperture was described and figured by Glaessner (1936, p. 117, pl. 2, figs. 9, 14). No internal plates or tubes are visible.

The characters as now described suggest a close relationship of *Amphimorphina* and *Plectofrondicularia*, as stated by Glaessner (1936, p. 120; 1945, p. 138) and Pokorný (1954). Because of their striking morphological similarity, the two genera are here placed in the *Plectofrondiculariinae*.

The type species of *Nodomorphina* Cushman, 1927, is *Nodosaria compressiuscula* Neugeboren, 1852. No specimens of this species were available in the U. S. National Museum. However, the generic diagnosis given by Cushman strongly suggests that this genus is synonymous with *Amphimorphina* Neugeboren. The only difference cited by Cushman is the complete uniseriality of the test (the quadrangular section of the test in the early stage is a common character in *Amphimorphina* also). But most specimens of *Amphimorphina* are megalospheric, and also show an uniserial arrangement of the chambers. The similarity of all the other characters suggests much doubt as to the separate validity of this generic name, and its suppression is recommended.

Family Buliminidae Jones, 1876

Subfamily Bolivinitinae Cushman, 1927

Genus Bolivinoidea Cushman, 1927

PLATE 33, FIGURES 14-16

Bolivinoidea CUSHMAN, Contr. Cushman Lab. Foram. Res., vol. 2, p. 89, 1927.

TYPE SPECIES: *Bolivina draco* Marsson, 1878, *Creatae* Weisses Schreiberkreide, from the Isle of Rügen, Germany.

DIAGNOSIS: Test biserial from the early stage, cuneiform, gradually increasing in breadth, with final chamber umbonate. Initial chambers near the proloculum more or less arched, and sometimes enveloping. Sutures oblique, slightly curved, at a 45-degree angle with the horizontal, thickened, flat. Wall calcareous, minutely perforate, internally tuberculate, and externally costate and tuberculate, giving a generally strong longitudinal ornamentation. Aperture narrow, generally basal, symmetrical, frequently provided externally with a lamellar lip and internally with a columellar toothplate, disposed axially between the two series of chambers and extending from the proloculum.

DISCUSSION: This Cretaceous and Paleocene genus was incompletely described, and was originally placed in the Heterohelicidae. This systematic position was corrected by Glaessner (1945) who placed the genus in the superfamily Buliminidea, family Buliminidae, subfamily Bolivinitinae, considering *Bolivinoidea* only a subgenus of *Bolivina*. The same position was accepted by Sigal.

In the last few years Hiltermann and Koch (1950), Reiss (1954) and Edgell (1954) published statistical researches on the stratigraphical variability of this genus, with particular attention to the variability in shape and ornamentation. Hofker (1952) noted the existence of a "toothplate" and attempted a reconstruction of the internal structure of the test.

The present work partially confirms Hofker's results, and gives some new structural information. The biseriality of the early stage is confirmed. Hiltermann and Koch (1950, p. 598) suppose that "der scheinbar planispirale Aufbau der Embryonal-kammern findet sich nach unseren Material nur bei einem kleinen Teil der Individuen und ist auch bei megalospherischen Formen zu beobachten." The simulated appearance of a coiled initial stage can be explained, because in the most extended forms of this genus, as for instance, *Bolivinoidea draco draco* (Marsson), the first two chambers formed after the proloculum are almost completely enveloping, in both the micro- and megalospheric forms. Actually, the biseriality is a constant character.

The aperture was correctly described by Hofker. In the specimens observed, the aperture is proportionally narrower and more reduced than was figured by Hiltermann and Koch. Furthermore the margin of the aperture is reduced at the surface to a thin lip, which can become lamellar in the better preserved specimens. This lamellar lip is not continuous, but is generally situated on the side opposite to that of the toothplate. The aperture is surrounded by a narrow depressed area.

The toothplate is externally visible in many specimens. Internally it is modified to form a tubular columella, which is visible in the figured sectioned specimen (fig. 14), and also in others not here figured but prepared with acid by the writer (Cushman Coll. 16267, 12108).

Hiltermann and Koch (1950, p. 597) described the internal structure as follows: "jede Kammer überdeckt die darunter liegende mit ihrer aussen etwas herabgezogenen Kammerbasis; die Einzelkammern besitzen eine Anzahl zu ihrer Basis rechtwinklig angeordnete Kammervertsätze, die auf die darunter liegende Kammer übergreifen; diese bilden die Skulptur und treten als Knoten oder Rippen auf. . . ; die Suturen werden dadurch entsprechend verdeckt und sind bei ausgesprochenen Rippenskulptur sogar unsichtbar. . . . Kammerraum langlich halbmondförmig; Anfangsteil verjüngt, manchmal etwas verdreht."

Hofker (1952, p. 379, figs. 3 and 4) gives an interpretation which needs correction. His figure 3b indicates thin sutures crossed by perpendicular processes. In figure 3c ("in optischen Schnitt") septal marginal folds

are drawn ("Überlappungen"), with correspondent costae ("darüber ungelagerten Kalkrippen"). His figure 4b shows the same character.

Some new internal characters were recognized in the present study. Specimens were examined in transmitted light at $\times 216$ magnification, and in order to obtain more complete evidence of the septal surfaces, some specimens were progressively acid-treated until final dissolution of the septa allowed an examination of the internal surface of the wall. In longitudinal section the chambers are semilunar or strongly arched, depending on their position as related to the proloculum and to the lateral extension of the test. The septa are very thick; they have often the same thickness as the chamber cavities themselves in the young stage; in the adult stage they gradually become thinner. The septal surface is flat, not undulated. The marginal undulation is simulated by the septa encountering an internally tuberculate wall (fig. 14). The large tubercles are present also in the central area and are aligned with the external sculpture.

In conclusion, the present investigation confirms the validity of the genus *Bolivinoidea* Cushman. It should not be placed near *Bolivina*, because of its very distinctive characters, the structure of the wall, sculpture, test shape and proportion, and it comprises an homogeneous group of species with a distinctive stratigraphical development.

Hiltermann and Koch (1950, p. 626) consider *Bolivina watersi* Cushman as an extreme form of *Bolivinoidea*. However, *B. watersi*, which has a neck and terminal aperture, has recently been made the basis for a distinct genus, *Trachelinella* Montanaro Gallitelli.

Genus *Bolivinita* Cushman, 1927

PLATE 33, FIGURES 17-20

Bolivinita CUSHMAN, Contr. Cushman Lab. Foram. Res., vol. 2, p. 90, 1927.

TYPE SPECIES: *Textilaria quadrilatera* Schwager, 1866, Lower Tertiary, from Kar Nikobar, "British India."

DIAGNOSIS: Test biserial, elongate, gradually enlarging in size, rectangular in transverse section and more or less compressed, with four strongly developed and sometimes lamellar axial costae at the angles; broader sides flat or moderately concave. Chambers elongate, irregularly pyriform or reniform, more inflated laterally. Earliest chamber with one basal spine in the microspheric and two or more spines in the megalospheric forms. Sutures straight and thin at the narrow sides, occasionally strongly limbate and oblique in the broader faces, where they form an angle of about 90 degrees, strongly arched and fused one to another at the lateral end of the broader faces, forming the lamellar longitudinal costae. Wall thin, calcareous, completely covered with minute pores and sporadic larger ones; frequently spinose and sometimes vertically costate in the early stage. Aperture basal, subcircular, elliptical, with major axis perpendicular to the suture and pro-

vided with a fairly well developed lip which may be present also in the sutural area. Apertural tooth moderately or not projecting, somewhat arched at the upper surface, enlarged internally in an oblique spout (toothplate), which is developed along either one or another of the sides of the chamber, and may be spatulate at the free lower end.

DISCUSSION: A plesio-type incorrectly figured by Cushman is here refigured. The other specimens are similar to those studied and illustrated by Hofker (1951b, p. 104) for comparison in following his morphological and structural studies. They probably represent a different species but the generic characters are constant. The results obtained by Hofker concerning the toothplate were substantiated, but other new structural details were also observed. The plate is variable in size, concavity, position in the apertural cavity, and development of the final spatula. One correction is necessary. Text-fig. 61d of Hofker (1951b, p. 105) represents the aperture limited in the ventrodorsal direction by a strongly limbate, arched septum. Not one of the approximately one hundred specimens of *Bolivinita quadrilatera* investigated from a single sample present such a character. In fact, the anterodorsal portion of the septum between the penultimate and the final chamber is not visible externally because it is situated internally to the aperture; the arch of the aperture ends in contact with a fold of the upper terminal surface of the penultimate chamber.

The conclusion of Hofker (1951b, p. 102) as to the systematic invalidation of this genus and its placement within the genus *Bolivina* seems hardly acceptable, at least until more is known about the importance of the toothplate, and until a correlation between the variability of this structure and that of other morphological characters is established. Investigations at high magnification, by thin sections and dissections, even in very minute specimens now show that internal processes are more common than was previously suspected, and we need much more evidence before establishing a new systematics on this basis alone. Furthermore, a systematics based only on toothplates and pores cannot consider the vast number of fossil Foraminifera where these characters are lacking or concealed by the process of fossilization, or obscure due to their minute size. Without further evidence, such a revision would result in confusion rather than order.

The toothplate represents only a single character, just as does the position and form of the aperture, the chamber arrangement, or the chamber shape. In a group of specimens from a single sample, the position, development, and shape of the toothplate may be quite variable.

Hofker (1951b, p. 107) stated "There is no reason why we should create a new genus only distinguished from the central genus by an ornamentation of the wall." Nevertheless, the presence of four vertical carinae is more than a question of ornamentation; it is the consequence of a completely different chamber shape. The chambers in *Bolivina* are generally reniform

or more or less depressed and are more inflated toward the axis of the test. In *Bolivinita* the chambers are pyriform in section, but have the more inflated portion at the external side of the test. This gives rise to flat or even concave broader faces of the test, and the strongly oblique chambers allow the lateral fusion of the limbate frontal sutures to form four vertical costae or lamellae. This character is present in different genera (*Bolivinitella*, *Eovigenerina plummerae*) which are easily distinguishable by such other morphological elements as the aperture and the chamber arrangement.

For these reasons, an invalidation of the name *Bolivinita* seems at least premature, and it is here recognized as a valid genus.

Genus *Tappanina* Montanaro Gallitelli, 1955

PLATE 33, FIGURE 21

Tappanina MONTANARO GALLITELLI, Mem. Accad. Sci. Lett. Arti Modena, ser. 5, vol. 13, p. 18, 1955.

TYPE SPECIES: *Bolivinita selmensis* Cushman, 1933, Upper Cretaceous Selma chalk, from New Corinth highway, 13.5 miles South of Selmer, McNairy County, Tennessee.

DIAGNOSIS: Test biserial, rectangular or rhomboidal or deformed in transverse section. Chambers depressed, cuneiform, apparently concave on the broad sides, more or less inflated laterally, with a well developed and sometimes fringed or lamellar carina which is horizontal or arched on the lateral margin then deflected and paralleling the long axis of the chambers. Sutures thin, depressed, straight or arched. Wall calcareous, finely perforate. Surface appears rough when carinae are strongly developed. Aperture narrow, elongate, at the center of the base of the last chamber.

DISCUSSION: The cuneiform shape of the adult chambers, with laterally subhorizontal or arched carinae, the deflection of the carinae on the broader faces, giving a rectangular transverse section to the test, and the independence of the carinae from the sutures are constant characters of this genus. Variable characters are the lateral convexity of the chambers, the development of the carinae and the more or less angular deflection at the beginning of the broader faces, and the deformation of the test in section from rectangular to rhomboidal or elliptical.

The group of forms allied to the type species have fundamentally different characters than do either *Bolivinita* Cushman or *Bolivinitella* Marie. Distinctive elements peculiar to the genus *Tappanina* are the presence of strong horizontal carinae, the narrow and deep sutures, the degeneration of the four axial lamellar sutural costae, characteristic of *Bolivinita* and *Bolivinitella*, into discontinuous thickenings and the character of the aperture.

Neither Cushman nor the later authors who examined specimens of this widespread species (*Tappanina selmensis* has also been found in the Upper Cretaceous and Paleocene of Europe) recognized the actual distinction

between the lateral thin sutures and the strongly developed horizontal arched carinae, which are relatively close to the preceding suture, and which give the tectiform appearance to the test.

The description of *Bolivinita selmensis* given by Cushman (1946, p. 114) is as follows: "Test minute, gently tapering from the subacute initial end, broad faces distinctly concave, the narrow sides strongly convex; chambers distinct, increasing gradually in size as added; sutures distinct, somewhat limbate; wall smooth, very finely perforate, translucent, especially in the middle of the chambers on the flattened faces; aperture narrow, at the inner margin of the last-formed chamber."

An analogous description was given for the very similar *Bolivinita costifera* Cushman (1946, p. 115): "Test small, about twice as long as broad, gradually tapering from the subacute initial end to the greatest breadth slightly above the middle, thence tapering slightly to the apertural end, periphery broadly rounded, strongly serrate in front view, in transverse section somewhat rhomboid, broader faces flattened or concave; chambers very distinct, increasing gradually in size as added, earlier chambers flattened and compressed, later chambers concave on the broader faces, and convex on the periphery, greatly increasing in thickness; sutures distinct, slightly curved in the early stages, more strongly so in the adult, slightly limbate; wall smooth and polished, except for the basal angle of the chamber in the adult, which has a sharp angle that may develop into a raised costa-like ridge; aperture narrow, elongate, at the base of the inner margin of the apertural face."

The holotype of *Tappanina selmensis* is here refigured. The holotype of *Eovigenerina excavata* Cushman consists of a specimen of *T. selmensis* with the last chamber broken and thus simulating a neck. This confirms the doubt of Brotzen (1948) about the validity of the species *excavata*. Only a "paratype" of the species *selmensis*, figured by Cushman and refigured by Brotzen (1948, text fig. 16, specimen on the left) is perhaps a true *Bolivinita*, characterized by the slender test and the typical sutures and sculpture, but the absence of other specimens compels a further investigation as to the existence of a toothplate.

Brotzen proposed a list of synonyms for *selmensis*: *Bolivinita crawfordensis* Jennings, *B. exigua* Glaessner, *B. costerifera* (read *costifera*) Cushman. However, after examining many paratypes and hypotypes from the Kemp Clay, the writer believes *Tappanina costifera* to be a valid form, although closely related to the type species. *B. exigua* Glaessner from the Upper Cretaceous of the Caucasus appears from the figures and descriptions to be a synonym of *T. selmensis*. *B. crawfordensis* Jennings, from the lower Eocene of New Jersey, cannot be satisfactorily compared with *T. selmensis* because of the insufficient description and figure of the former.

In addition to the holotype of *Tappanina selmensis* (Cushman), the writer (Montanaro Gallitelli, 1956,

pl. 7, figs. 3-7) recently refigured the conspecific "holotype" of *Eouwigerina excavata* Cushman, and the holotype and two hypotypes of the congeneric *T. costifera* (Cushman), hence these are not here refigured.

Subfamily Eouwigerininae Cushman, 1927

Genus *Eouwigerina* Cushman, 1926

PLATE 34, FIGURES 1-7

Eouwigerina CUSHMAN, Contr. Cushman Lab. Foram. Res., vol. 2, p. 4, 1926.

TYPE SPECIES: *Eouwigerina americana* Cushman, 1926, Upper Cretaceous Taylor marl, from pit of Dallas Brick Company, ½ mile west of Mesquite, Dallas County, Texas.

DIAGNOSIS: Test small, biserial throughout, commonly twisted and thus may simulate an appearance of triseriality. The chambers immediately following the proloculum are reniform and arranged longitudinally on opposite sides of the proloculum, giving a round outline and a false coiled appearance to the neanic stage. In the adult the commonly loosely arranged chambers are more inflated, assuming a pyriform or, if carinate, subtriangular shape. When the chambers are overlapping and carinate, the test becomes subrectangular in cross section. The final chamber is nearly central in position. Wall calcareous, surface finely perforate and frequently more or less spinose. Strong carinae may be present in the mature stage, following the length and the curvature of the chambers and consequently becoming horizontal, arched and finally subvertical or vertical.

Aperture terminal, with a more or less well developed neck and lip. One or two thin transverse ridges may appear on the surface of the neck. Internally the aperture has a thin columellar process (fig. 2) which is also visible in the young stage.

DISCUSSION: Loeblich (1951, p. 109), after restudying the types, substantiated the description of Glaessner (1945, p. 138), correcting the original generic diagnosis of Cushman by recognizing the absence of a coiled early stage, and the complete biseriality of this genus, tending to a uniserial development.

The use of high magnification and numerous partially acid-treated specimens in the present study revealed the presence of an internal columellar process, extending from the very young chambers of the test up to the aperture. Because of the small size of the test, the tubular nature of this process is visible only in the last chamber and the shape of this very thin "toothplate" and the position of its departure from the aperture could not be determined.

Another investigation of some interest concerned the relationship of the external shape in the different species of *Eouwigerina* to the (1) shape and position of each chamber, and (2) presence, position and development of the carinae, which are more or less well developed in nearly all the species.

There is a great variability in the form of the test,

and a separation into different species often cannot easily be made. If the Paleocene species *Eouwigerina excavata* Cushman, which is conspecific with *Tappanina selmensis* (Cushman), is excluded, it can be said of *Eouwigerina* that the test is frequently twisted, a fact that lead Cushman and others to believe it triserial; and the change in shape in the mature stage is gradual, and is related to the development and the overlap of the pyriform chambers, and the strength of the carinae. An example without carinae is *E. fragilis* (Terquem), which has uvigeriniform later chambers. When the carinae are strongly developed, the pyriform chambers become subtriangular in top view, which may lead to different test shapes, according to the more or less close arrangement of the chambers. Chambers closely arranged and carinate, but not large or much arched, have a *Tappanina*-like appearance, subrectangular in cross section and depressed on the broader faces, as in *E. serrata* (Chapman) and *E. americana* Cushman (part). When the chambers are carinate, loosely arranged, twisted (as in USNM P4887), and tend to become almost uniserial, a false triserial appearance is given, when viewed from above, as in typical *E. americana* Cushman.

Eouwigerina plummerae is a very distinctive form. As the present research is an analytical restudy of the genera as based on their type species, a discussion of each species is out of place. Nevertheless as some "transitional" specimens are in the U. S. National Museum, it is perhaps of some interest for further discussion to show such specimens, and two aberrant specimens of *E. americana* for comparison. If this species belongs to another genus—as there is evidence to believe—it must in any case be related to *Eouwigerina*. The chambers are elongate and strongly arched, losing the lateral portion of the carinae (as is also true in aberrant *E. americana*, figs 3, 5), become closely appressed and overlapping, with fusion of the arched carinae on the sides of the broader faces from the early stage, giving four sharp vertical *Bolivinita*-like lamellae, although the species is clearly distinguishable from *Bolivinita* by the different aperture. An appearance of similarity seems to exist between *E. plummerae* and *Bolivinitella*. Nevertheless the latter genus has a quite different aperture and lacks an apertural or columellar process.

The results of the studies of this genus by Glaessner (1945), Loeblich (1951) and the present study all show clearly that neither the morphological nor structural characters of *Eouwigerina* show any relationship to the true Heterohelicidae.

Genus *Siphogenerinoides* Cushman, 1927

PLATE 34, FIGURES 8-10

Siphogenerinoides CUSHMAN, Contr. Cushman Lab. Foram. Res., vol. 3, p. 63, 1927.

TYPE SPECIES: *Siphogenerina plummeri* Cushman, 1927, Upper Cretaceous, Maestrichtian, from bank of Walker Creek, 6 miles N.15° E. of Cameron, about 1

mile upstream from intersection of Walker Creek and Cameron-Clarkson road, Milam County, Texas.

DIAGNOSIS: Test elongate, straight, constantly biserial in the early stage in both microspheric and megalospheric forms. Chambers rather inflated. Sutures slightly depressed, subhorizontal. Wall calcareous, perforate, surface crossed by numerous continuous costae, which may become lamellar and thickened near the sutures. Aperture terminal, elliptical or reniform, frequently interrupted by fusion with the columellar spout, which is arched in cross section and may rarely give the appearance of two teeth. Columellar process well developed, spoutlike in shape, developed from the early stage, each successive simple intercameral spout with its concave side facing in the opposite direction to that of the spout immediately preceding, and each apertural lip, except that of the final chamber, connects to the extremities of two sections of spout, the terminal end of the inferior one and the base of that in the succeeding chamber situated diametrically opposite in the circular opening and both having their convex surface oriented toward the opening.

DISCUSSION: A study of numerous topotypes was made. Acid-treated specimens show clearly the characters of the "siphon" described by Plummer (1931) and Stone (1946) and of the early stage. The early stage is always biserial, even in megalospheric forms. No specimen showed a triserial beginning. The biserial stage is very short in the megalospheric forms (2 to 6 chambers), and more fully developed in microspheric ones (as many as 10 chambers).

A longitudinal acid-section shows (fig. 10) the internal alignment of the columellar process. The section was purposely not completely axial, and the previous interpretations of the internal structure are corrected as follows: The internal process is not a "tube" as described by both Plummer and Stone, who gave extremely small figures; it is an hemicylindrical subvertical process (spout), joining from one opening to another of two adjacent chambers. The spout always lies with the convexity oriented toward the apertural opening and is not continuous; there are single sections for each chamber, and each opening, except that of the last chamber, receives on one side the terminal portion of one section of spout and on the other side the beginning of the superjacent one. This alignment is very regular and is shown in the figures.

The position and the direction of the convexity of the spout explains the secondary small opening observed by Plummer. The aperture of the last chambers receives only the end of one section of spout. In the region of the termination of the spout the apertural lip may be reduced or absent, and the section of the end of the spout (which has the convexity facing the aperture) may be secant and simulate a second small opening. According to the different position of adherence of the spout to the apertural lip, different shapes of apertural outline (subcircular, reniform, irregular) may arise.

A relationship of *Siphogenerinoides* with triserial genera must be excluded. The presence and the nature of the columellar process, the biseriality of the early stage, and the apertural features are the characters important for its systematic placement. According to the present morphological revision, a close relation with *Siphogenerina* now appears probable. Only the character of the columellar process seems still to distinguish *Siphogenerinoides* from *Siphogenerina*. Sigal (1952, p. 219, fig. 80, p. 220, pl. 16, figs. 17a,b) states that *Siphogenerinoides* (which he includes in the Uvigerininae, with triserial initial stage) has the columellar process "external" to the aperture, instead of "internal" as in *Siphogenerina*. A further investigation as to the variability of the joining position of the columellar process to the aperture in both *Siphogenerina* and *Siphogenerinoides* is recommended.

Genus *Zeauvigerina* Finlay, 1939

PLATE 34, FIGURES 11, 12

Zeauvigerina FINLAY, Trans. Proc. Roy. Soc. New Zealand, vol. 63, p. 541, 1939.

TYPE SPECIES: *Zeauvigerina zelandica* Finlay, 1939, middle-upper Eocene, Danneverke area, New Zealand.

DIAGNOSIS: Test small, subcircular to elliptical in cross section. Chambers biserially arranged, minute and depressed in the early stage, rather inflated in the mature stage; sutures horizontal to oblique, with an angle of up to 15 degrees from the horizontal. Final chamber frequently less inflated than the penultimate, flask-shaped, tending to become central and provided with a neck, which is commonly almost as large as the last chamber. Apertural margin proportionally thick, circular or elliptical, internally provided with fine tuberculate ridges, commonly reducing the aperture to an elliptical opening. Wall calcareous, surface fairly rough, rarely finely spinulate.

DISCUSSION: Only three paratypes were available in the U. S. National Museum collection, consequently an analysis of the internal structure of the test was practically impossible. Finlay based the separation of this genus from *Eouvigerina* Cushman on the complete biseriality of the new genus, compared to the "coiled" first stage and the "triserial" arrangement of the mature stage in *Eouvigerina*. The critical review made by Loeblich (1951) recognized that neither coiled early stage nor triseriality are present in *Eouvigerina*. Consequently, Loeblich considered *Zeauvigerina* a synonym.

The present investigation revealed the presence of a toothplate in *Eouvigerina*. The same internal character may be present in *Zeauvigerina* also, but it is still unrecognized; the three paratypes examined are internally filled with sand, and an investigation by transmitted light was inconclusive.

If all external characters were identical to those of *Eouvigerina*, the generic name of Finlay doubtless should be invalidated, and the problem of the presence of the toothplate set aside for the present, as we do not yet know how widespread is this single character in the

smaller Foraminifera, nor what is its systematic importance. But in *Zeawigerina* (at least in the paratypes studied) the chambers are strongly compressed, with almost horizontal sutures, instead of having the rather loosely appressed chambers of *Eouwigerina*; the last chamber is smaller in size than the penultimate in *Zeawigerina*, the neck is considerably larger and the apertural cavity more reduced than in *Eouwigerina*. Consequently, these features have led the writer to maintain, although with many doubts, the name *Zeawigerina*, until a complete structural, morphological, and, if possible, statistical investigation of abundant material of both "genera" is made, showing transitional forms between the two populations.

Genus *Trachelinella* Montanaro Gallitelli, 1956

PLATE 34, FIGURE 13

Trachelinella MONTANARO GALLITELLI, Contr. Cushman Found. Foram. Res., vol. 7, p. 38, pl. 7, figs. 8-10, 1956.

Trakelina MONTANARO GALLITELLI, Mem. Acad. Sci. Lett. Arti Modena, ser. 5, vol. 13, p. 5 (nomen nudum), 1955.

TYPE SPECIES: *Bolivina watersi* Cushman, 1927, Upper Cretaceous Navarro (Maestrichtian), Core A-D-1 (Sun Oil Co.), from east of Richlands, Navarro County, Texas.

DIAGNOSIS: Test elongate, flaring gradually, commonly twisted as much as 90 degrees, thickest in median line; periphery subacute, generally carinate, or more rarely serrate. First chamber with a basal spine and rarely two opposing median costae; adult chambers strongly arched. Sutures narrow, arched, deep. Wall calcareous, finely perforate, smooth. Sculpture well developed, with prominent, rough, somewhat spinose carinae, aligned along the major extension and inflation of the chambers and consequently strongly arched, commonly fused at the lateral margins, which become carinate or serrate. Aperture terminal, round or slightly elliptical, with a short neck and a lip. No apertural internal teeth visible, at a magnification of more than 200 diameters.

DISCUSSION: This genus is very abundant in the Upper Navarro Kemp clay. The holotype of "*Bolivina*" *watersi* Cushman is a specimen with a broken apertural neck, giving an erroneous *Bolivina*-like appearance. A short apertural neck is visible at high magnification on one of the two broad faces of this specimen.

This genus differs from *Bolivina* in the presence of a well developed neck which may relate it to the *Eouwigerinae*. The oblique axis, the short neck of the last chamber, and the biserial arrangement of the chambers also suggest a relationship with *Bolivinitella*, although the latter genus has a peculiar rectangular section, concave broader faces, and four vertical lamellar costae, features not characteristic of *Trachelinella*.

Additional specimens of the type species were recently figured by the writer, hence are not here refigured.

Genus *Bolivinitella* Marie, 1941

PLATE 34, FIGURES 14-17

Bolivinitella MARIE, 1941, Mem. Mus. Hist. Nat., new ser., vol. 12, p. 139.

TYPE SPECIES: *Bolivinita eleyi* Cushman, 1927, Upper Cretaceous Brownstown marl, 8.1 miles west of Arkadelphia, Clark County, Arkansas.

DIAGNOSIS: Test elongate, biserial throughout, rectangular in section and compressed. Broader sides flat or concave, chambers reniform, strongly overlapping and arched in the mature stage, tending to become uniserial. Last chamber strongly compressed at the upper portion. Sutures limbate, strongly arched on the broad sides and fused at the four angles to form four longitudinal carinae. Aperture terminal, linear or elliptical, may have a lip, the apertural cavity finely tuberculate.

DISCUSSION: Hofker's peculiar conclusions concerning this genus are not supported by sufficient observation. He invalidated the present generic name and placed *Bolivinitella* with *Siphogaudryina*, which has, however, an arenaceous test and a triserial early stage. As the test of *Bolivinitella* is calcareous and soluble in dilute hydrochloric acid, a diagnosis of the so-called secondary material (granules) by optical and X-ray methods is required. When partially acid-treated the test shows a transparent shell material at high magnification.

Dissections by acid and observations of the generation B of Hofker did not show any triserial early arrangement of the chambers in any of the numerous specimens in the National Museum collections. However, a strongly tuberculate or more rarely costate ornamentation at the beginning of the test is very frequent.

The absence of a toothplate is substantiated, not unexpectedly, because of the extremely thin anterodorsal section of the final portion of the last chamber. If a toothplate is present in the young stage (because of the smallness of the specimens, this could not be demonstrated at X 216 magnification or by acid-treatment) it must be obviously absent in the apertural extension of the chamber. The aperture is not exactly as described by Hofker, but is more frequently linear and occasionally elliptical, and provided with a lip. In the best preserved specimens the lip shows internally a relatively well developed granulation which may obliterate the aperture and perhaps even cause it to become cribrate.

For these reasons the consideration of *Bolivinitella* as a synonym of *Siphogaudryina* is discounted, and the genus is here held to be valid. The position and feature of the aperture, and the shape of the chamber are constant and distinctive generic characters, despite the absence of the toothplate.

? Family Buliminidae Jones, 1876

Genus *Tosaia* Takayanagi, 1953

PLATE 34, FIGURE 18

Tosaia TAKAYANAGI, Inst. Geol. Paleontol. Sendai, Short Paper No. 5, p. 30, 1953.

TYPE SPECIES: *Tosaia hanzawai* Takayanagi, 1953, Pliocene Nobori formation, from cliff 100 miles east of Nobori, Hane-muri, Aki-gun, Kochi Prefecture, Japan.

DIAGNOSIS: Test rapidly enlarging, triserial or occasionally biserial in last three chambers. Early stage obscure, not improbably trochoid. Early chambers depressed, rather inflated, last three or four chambers more inflated, with sutures consequently more depressed. Wall calcareous, smooth, finely perforate. Aperture basal, relatively small, provided with a fairly rough lip.

DISCUSSION: Only three specimens were available for the present investigation: one relatively large paratype here figured, and two smaller, completely triserial specimens. Consequently very little can be added to the original diagnosis and only a statistical investigation as to the variability of this genus can decide if the final biserial arrangement is an aberration or not.

Takayanagi compares this genus to *Guembelitria*, of which the triserial arrangement and the basal aperture are suggestive; that the triseriality is only a matter of convergence is shown by other important characters, namely: the reduction to a biserial arrangement in the final stage; the vertical compression of the young chambers, resulting in subhorizontal sutures; the extension of the wall in a liplike plate at the aperture (without the compact structure of the usual lip); and, finally, the much larger test than in *Guembelitria*, which is characterized by its very small size. A very uncertain character, at present, is the arrangement of the early chambers. The specimens available were too scarce, so that a partial dissolution by acid-treatment was impossible. Immersion in anise oil seems to reveal a trochoid early portion, although this appearance may be due to reflections, and further investigation of numerous and well preserved specimens must be awaited.

Family Uvigerinidae Galloway and Wissler, 1927

Subfamily Uvigerininae Galloway and Wissler, 1927

Genus *Pseudouvigerina* Cushman, 1927

PLATE 34, FIGURES 19-22

Pseudouvigerina CUSHMAN, Contr. Cushman Lab. Foram. Res., vol. 2, p. 81, 1927.

TYPE SPECIES: *Uvigerina cristata* Marsson, 1878, Cretaceous of Rügen Island (Pomerania). Figured hypotype from the Upper Cretaceous, Gerhardsreuter Schichten (Maestrichtian), Starzmühl near Teisendorf, Upper Bavaria, Germany.

DIAGNOSIS: Test small, triserial throughout, triangular in cross section. Chambers normally inflated, externally triangular in section because of the presence of three strong double vertical costae disposed along the line of major inflation of the chambers. Sutures limbate, distinct, slightly depressed; between the sutures the wall is covered by numerous tubercles, which may become well developed and proportionally large. Aperture circular or subelliptical, with a short neck. Internally, a narrow columellar plate is developed from the early stage, and connected to the aperture (where no tooth is visible).

DISCUSSION: Cushman described an early biserial stage for *Pseudouvigerina*. An investigation of hypotypes from the Upper Cretaceous of Bavaria showed the early stage to be triserial in both generations.

Furthermore, a partial dissolution by hydrochloric acid revealed the presence of an internal plate, somewhat oblique and free at its lower end. The plate has no tooth at the apertural end, but terminates at the base of the neck.

The genus *Pseudouvigerina* possesses no characters for separation from the Uvigerininae. A generic identity of *Angulogerina* with *Pseudouvigerina* is at present only suspected. Sigal (1952, p. 219) follows Galloway in stating that *Angulogerina* differs from *Pseudouvigerina* in tending to become uniserial. No comparison in this respect between species of both genera has been made here to confirm this difference. If a tendency to become uniserial should be demonstrated also in *Pseudouvigerina*, *Angulogerina* would become a junior synonym of *Pseudouvigerina*.

Class Crustacea

Order Isopoda ?

Genus *Nodoplanulis* Hussey, 1943

PLATE 34, FIGURE 23

Nodoplanulis HUSSEY, Journ. Paleontol., vol. 17, p. 166, 1943.

TYPE SPECIES: *Nodoplanulis elongata* Hussey, 1943, Eocene, Cane River formation, La Salle Parish, Louisiana.

DIAGNOSIS: Test elongate, transparent, depressed, with lateral margins parallel. Basal portion flat, depressed, provided with a series of four or five complanate spines. The test consists of six vertically arranged sections; on the base of each a crown of irregularly developed, rarely spinate tubercles is present. Each section appears separated from the others at the surface by a variable and irregularly developed band. The upper end is provided with a "neck" and terminates in an elongate aperture with lip.

DISCUSSION: Only the holotype was available for study; consequently no sections to show the internal structure were made. Nevertheless the good preservation of the fossil allows some discussion of the diagnosis given by Hussey.

The specimen does not show any spiral early stage. Immersed in anise oil it shows only a spinulate, compact basal region, followed by a single hollow section of the test. No traces of sutures appear in transmitted light, nor is there any suggestion of minute chambers, spiral or otherwise. The arrangement is then, in any case, uniserial. The "sutures" are not clear; they are neither limbate nor linear, but appear like a band of opaque material, variable in size in the different positions but not regularly enlarging from the base to the top. The absence of other specimens prevented the preparation of thin sections to determine if septa are present internally. Viewed in transparency this character is

concealed. At the top, a flat neck is provided with a lip and an elliptical narrow opening.

Because of the obscure morphology of the "sutures" and of the other general characters of the specimen (base with comblike arrangement of spines, character of the tubercles at the base of each segment) some doubt arose as to the actual foraminiferal nature of this fossil. Dr. Fenner A. Chace, Division of Marine Invertebrates, U. S. National Museum, kindly agreed to examine this specimen and concluded that there were no characters preventing an interpretation of this fossil as the base of the flagellum (first or second antenna) of a Crustacean, probably an Isopod.

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